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Environmental controls on spatial variability of summer phytoplankton structure and biomass in the Bering Sea

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ABSTRACT

The subarctic Bering Sea, one of the most productive regions of the world's oceans, is undergoing significant ecological shifts possibly linked to global climate change. During the Fourth Chinese National Arctic Research Expedition (CHINARE) from July 10 to 20 of 2010, phytoplankton community structure, species diversity, spatial distribution, community types, abundance and biomass variations were investigated in a large scale study extending from the Bering Strait into the open waters down to the subarctic Pacific. These patterns were linked to potential environmental drivers, including effects of water masses and seasonal sea ice retreat. Results showed a marked spatial zonation in the taxonomic composition, abundance and biomass. A total of 149 phytoplankton taxa distributed among 57 genera of 5 phyla were identified, characterized into three ecological groups, namely Arctic, Boreal-temperate and cosmopolitan species. Phytoplankton included 101 species of diatoms, 44 species of dinoflagellates, 2 species of Chrysophyta, 1 species of each Chlorophyta and Euglenophyta. Both abundance and biomass were highest in the Bering Shelf, moderate on the Bering Slope, and lowest on the Bering Basin. Chlorophyll *a* was found highest in the subsurface chlorophyll maxima (SCM) close to the thermocline and halocline layers but its depth varied regionally. Multi-dimensional scaling (MDS) revealed two types of assemblages, one a deep-sea assemblage associated with the Bering Basin and a neritic assemblage found in the Bering Slope and Shelf. Average abundance (10.22×10^3 cells/L), biomass (0.43 mg/m^3), species diversity (2.60) and species richness (1.66) were established for deep-sea assemblage with the dominant species ranked as *Neodenticula seminae*, *Chaetoceros atlanticus*, *Pseudonitzschia delicatissima*, and *Thalassionema nitzschioides*. Neritic assemblage had higher values with 12.73×10^3 cells/L, 2.41 mg/m^3, and 2.55 species richness but lower (2.41) species diversity, and the community was mainly dominated by *Thalassiosira nordenskiöldii*, *Leptocylindrus danicus*, *Chaetoceros socialis*, *Chaetoceros debilis*, *Fragilariopsis oceanica*, *Nitzschia closterium* and *Chaetoceros furcellatus*. A diatom bloom was observed near the Bering Strait in the summer of 2010 induced by high availability of nitrate particularly in the Bering Shelf, while water mass transportation mainly influenced communities in the Bering Basin and Slope. The observed fluctuation in both biomass and summer phytoplankton communities in the Bering Sea were mostly influenced by events related to the spring sea ice retreat in 2010.

1. Introduction

The subarctic Bering Sea, the northern extension of the North Pacific Ocean, is one of the world's most productive oceanic regions (Iverson et al., 1979a). In recent years, increasing in air temperature, and dramatic decrease in the sea ice extent and thickness have occurred throughout the Bering Sea (Schumacher et al., 2003; Grebmeier et al., 2006), with great impacts on its local climate, oceanography and productivity (Alexander and Niebauer, 1981; Hunt et al., 2002). Despite, considerable inter-annual variation, at its annual maximum, sea ice can cover the entire Bering Shelf, extending to over an average of 200,000 km^2 before completely retreating that leads to ice-free summers (Wendler et al., 2013). With strong water column mixing mainly driven by interactions of wind, water masses and sea ice, the Bering Sea has very high surface phytoplankton biomass and primary productivity in spring, especially in the upper layer of northeastern Bering Sea Basin and northwestern Bering Slope to the edge of Bering Shelf, known as the “Bering Sea Green Belt” (BSGB) (Alexander and Niebauer, 1981; Springer et al., 1996). However, the center of the Bering Basin is iron-limited, making it a high-nutrient and low-Chl *a* (HNLC) region, with high nitrate and silicate concentrations all year round (Banse and English, 1999; Aguilar-Islas et al., 2007). Additionally, the surface

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circulations in the Bering Shelf and Basin differ significantly, appearing to have originated from two different water masses (Coachman, 1986; Walsh et al., 1989). Consequently, upwelling caused by tidal fronts and wind-driven mixing may extend the duration of spring blooms along the ice edge by supplying nutrients in the Bering Sea (Niebauer and Alexander, 1985; Lovvorn et al., 2009).

The photosynthetic diatom species are one of the most dominant groups found in the microbial communities of the Bering ecosystem. They are sensitive to changes in their environment such as sea ice and conditions in water masses, which influence both their diversity and assemblages (Motoda and Kawarada, 1955; Sukhanova et al., 2009). Semina and Jousé (1959) were the first to study pelagic diatoms in the western Bering Sea. From 1960 to 1980, several comprehensive systematic and bio-geographical studies on plankton in the central basin and northern shelf of the Bering Sea were also carried out (Motoda and Minoda, 1974; Werner, 1977; Heimdal, 1989). However, most studies on phytoplankton communities were mainly carried out in the western Bering Sea (McQuoid and Hobson, 1998; Hobson and McQuoid, 2001; Yang et al., 2002; Hay et al., 2003; Aizawa et al., 2005), and only a few were conducted in the eastern side (Taniguchi et al., 1976; Iverson et al., 1979a, 1979b; Schandelmeier and Alexander, 1981). Further, traditionally, these studies were done using microscopy (cell counts) and in situ measurements of biomass. A series of studies applying satellite multi-sensor remote sensing (Sei-ichi et al., 2002) have also been done to look at the effects of convective and wind-driven mixing (David and Richard, 2001), nutrient limitation (Suzanne and Kerri, 2008), microzooplankton grazing (Olson and Susanne, 2002) to gain further understanding of spring bloom dynamics in the Bering Sea.

Although Chinese scientists have conducted six Arctic scientific expeditions since 1999, the foci were mostly on pelagic bacteria, protozoa, picophytoplankton and other heterotrophic groups (He et al., 2005; Zou et al., 2009; Zhang et al., 2011; Liu et al., 2011). Studies on phytoplankton taxonomy and biomass of the Bering Sea have only been reported by Yang et al. (2002, 2006) during the First Chinese National Arctic Research Expedition (First CHINARE) in 1999 mainly on phytoplankton collected with a standard phytoplankton net with a pore size of 67-μm following Aikawa (1932), Motoda and Kawarada (1955). Then, reports on the ecological characteristics of the pelagic phytoplankton community (> 10 μm) followed in the eastern Bering Sea in 2009 (Wang, 2009).

Based on measured chlorophyll *a*, data set of phytoplankton community (> 10 μm) and nutrient data in the Bering Sea during the Fourth CHINARE in the summer of 2010, this work aims to (1) understand the spatial variability of communities and biomass of phytoplankton in the Bering Basin, Slope and Shelf, and (2) further enhance our understanding of the influences of water masses and seasonal sea ice retreat on the formation and maintenance of spring blooms, relative to the changes in the physical and chemical conditions of the region.

2. Material and methods

2.1. Study area and sampling stations

Samples used in this study were collected from different depths in the 18 stations in Bering Sea (169°E–166°W, 50°N–67°N) on board the research vessel Icebreaker *Xuelong* during the Fourth CHINARE from July 10 to 20 in 2010 (Fig. 1).The stations were strategically positioned in different oceanographic regions including the deep-sea basin (Bering Basin, 5 stations), continental slope (Bering Slope, 2) and shelf (Bering Shelf, 11).

2.2. Sample collection and data sources

A total of 1 L of seawater for phytoplankton samples was collected at discrete depths, specifically from the surface, 10, 20, 30, 50, 75, 100, 150, 200 m, with 12-L Niskin bottles mounted on a Rosette system and equipped with conductivity, density and temperature (CTD) profilers (SeaBird Electronics; SBE911 Plus) during the upcast. Phytoplankton samples were fixed by buffered formalin (final concentration 3%) and stored in darkness. In the laboratory, phytoplankton cells were concentrated with 50 mL settlement columns for 24 h, the identification and cell abundance was quantified using the Utermöhl settling method (Edler and Elbrächter, 2010). Counting was manually done under an inverted microscope (Zeiss-Z1, Germany) at 200 × or 400 × magnification following the UNESCO phytoplankton manual (Sournia, 1978). For scanning electron microscopy (SEM), Milli-Q water was used to rinse formaldehyde and salt in phytoplankton water samples, which were repeated many times until pH 7 was attained. Then a drop of phytoplankton water samples was placed on a glass cover-slip, air-dried, coated with platinum using a sputter-coater before being examined under an SEM (Hitachi TM-1000, Japan). Phytoplankton and other protists were enumerated and identified down to the species level following the descriptions and taxonomic keys previously described (Taniguchi et al., 1976; Hasle and Syvertsen, 1997; Okolodkov, 1999; Yang et al., 2002; Guo and Qian, 2003; Shimada et al., 2003; Irina et al., 2009; Lin et al., 2009). Identification and counts presented here only focused on cells > 10 μm, and zoomastigophora was not further considered.

Chlorophyll *a*, a proxy for phytoplankton biomass, was collected by filtering 500 mL of seawater through Whatman (25 mm) GF/F filters, and kept frozen at − 20 °C and in the dark for 24 h before extraction in 90% acetone and quantified using a fluorometer (Turner Designs 10-Au Fluorometer) as described by Yentsch and Menzel (1963).

From the same Niskin bottle as for the biological samples, 500 mL subsamples for nutrient analysis were processed immediately after collection. If not possible, samples were immediately refrigerated at 4 °C and then analyzed within 24 h upon sampling. In particular, nitrate (NO_3), nitrite (NO_2), ammonia (NH_4), phosphate (PO_4) and silicate concentrations were measured using a SKALAR SAN + + spectrophotometer following the methodology of Grasshoff et al. (1999).

2.3. Statistical analysis

Shannon-Wiener diversity (*H′*), Pielou's evenness (*J′*), species richness index (*d*) and species dominance index (*Y*) were calculated in the package PRIMER5.0 (UK). Bray-Curtis dissimilarity was then calculated to measure beta diversity between communities (samples), and visualized using cluster analysis and multi-dimensional scaling (MDS) in the same software. Taxa with occurrence < 10% were considered as variables in cluster analysis and MDS. Then, species abundance was square root transformed to standardize before comparison, which was then used to generate the dissimilarity matrix.

To link diversity and species patterns with environmental drivers, Pearson's correlations among and between phytoplankton biomass, abundance and environmental variables were determined in SPSS statistical software (Version 17.0 for Windows, Chicago, USA). A commercial software for multivariate statistical package (Canoco for Windows 5.0) was applied to carry out canonical correspondence analysis (CCA) between the biological group and environmental parameters including chlorophyll *a*.

3. Results and analysis

3.1. Oceanographic conditions

In July 2010, stratification driven by temperature differences typical of the Arctic Ocean was observed in the Bering Sea (Table 1), with the shallow water < 20 m depth being warm with temperature > 7 °C. A temperature maximum was observed at 20–30 m, followed by a sharp decrease towards the deeper layers reaching below 3 °C. Therefore, we assumed there was a strong thermocline from 20 m to 40 m, which could be pertaining to the Pacific Summer Water (PSW) or the

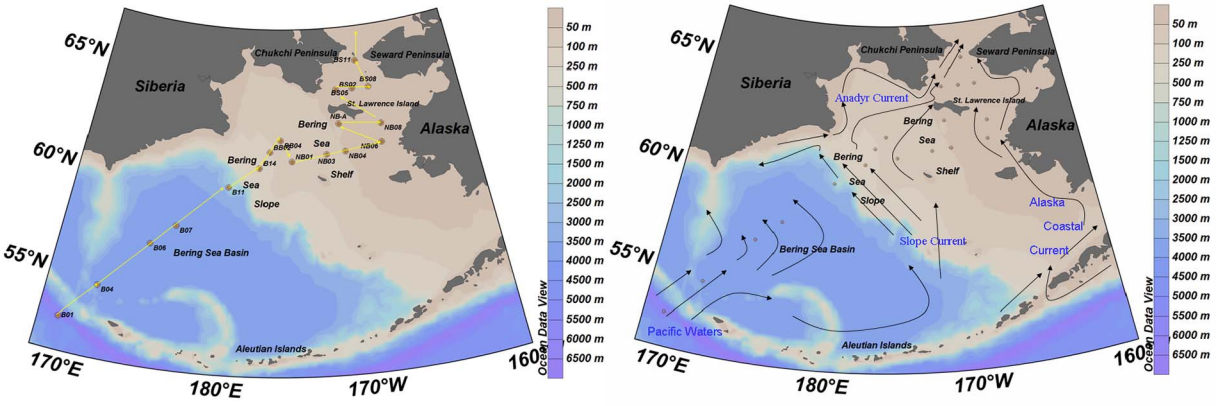

Fig. 1. Map of the Bering sea, showing cruise route, water mass types, spatial locations (modified from the map provided by Thomas R, Loughlin K, University of Alaska Sea Grant) and sampling stations for phytoplankton biomass and taxonomy during the Fourth CHINARE cruise performed onboard the R/V Xuelong icebreaker (10 July–20 July 2010). The study area covered the deep-sea basin (200 to 4000 m), slope (100 to 200 m) and shallow shelf (< 100 m). Water masses are mainly Pacific Waters, Alaskan Coastal Current, Slope Current and Anadyr Current.

remnant summer mixed layer.

The average surface concentrations of DIN (NO_3 + NO_2 + NH_4), phosphate and silicate in the Bering Sea were 2.10 μmol/L, 0.72 μmol/L, and 10.36 μmol/L, respectively. Higher values of these nutrients were found in the southern Bering Basin and nearby the Bering Strait. On the other hand, lower concentrations of nutrients differed regionally. Specifically, DIN was generally low (average 0.51 μmol/L) in the Bering Shelf, except in some stations (BS02, BS05), nearby the Bering Strait. Phosphate was lower in the Bering Slope but with slightly higher silicate on both Bering Slope and Shelf (< 1.04 μmol/L) (Table 1). A reasonable assumption is due to the high productivity during spring blooms that exhausted much of the nutrients in the photic waters, both surface DIN and silicate were almost unavailable in the Bering Slope and Shelf towards summer. In the shallow euphotic zone above 50 m, nutrients were observed to have high to low distributions from the Basin, Slope, and to the Shelf (Table 1). In contrast, nutrient concentrations near the Bering Strait were always higher than the average of the Bering Slope, except for the phosphate which was similar throughout.

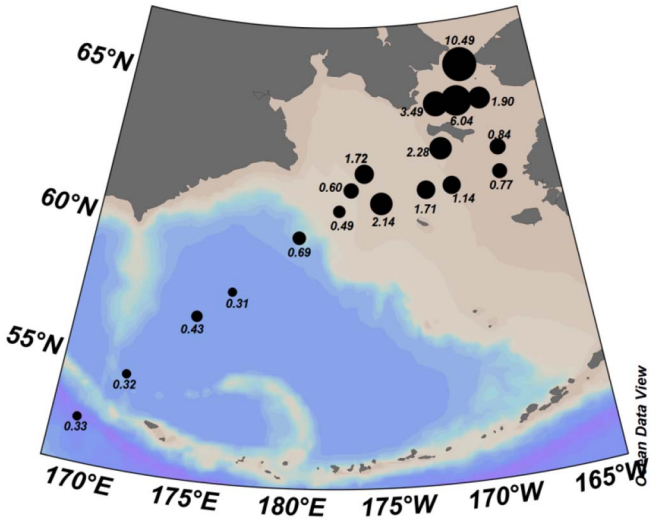

Fig. 2. Spatial distribution of average Chl *a* (mg/m^3) in water column of the Bering Sea in July 2010.

3.2. Phytoplankton biomass

As shown in Fig. 2, latitudinal distribution of Chl *a* in the water

Table 1
The spatial variability of environmental parameters and vertical distribution for each set of stations in the Bering Sea in July 2010 (average value of temperature/°C, salinity/psu, DIN/μmol/L, PO_4-P/μmol/L, SiO_3-Si/μmol/L).

Spatial	Basin	Slope	Shelf
Stations	B01, B04, B06, B07, B11	B14, BB02	BB04, NB01, NB03, NB04, NB06, NB08, NB-A, BS02, BS05, BS08, BS11
Surface	7.46 °C, 32.94 psu, 12.53DIN, 1.35P, 31.72Si	7.60 °C, 30.93 psu, 0.51DIN, 0.27P, 1.04Si	7.38 °C, 31.37 psu, 0.58DIN, 0.51P, 2.35Si
10 m	ND	7.43 °C, 30.92 psu, 0.52DIN, 0.34P, 1.15Si	6.37 °C, 31.35 psu, 0.50DIN, 0.58P, 2.25Si
10–20 m	ND	3.50 °C, 31.08 psu, 0.54DIN, 0.69P, 1.66Si	4.26 °C, 31.56 psu, 0.82DIN, 0.69P, 4.01Si
20–30 m	4.56 °C, 32.98 psu, 15.69DIN, 1.54P, 42.51Si	− 1.08 °C, 31.43 psu, 0.44DIN, 0.60P, 1.36Si	− 0.09 °C, 32.03 psu, 1.83DIN, 0.91P, 9.38Si
30–50 m	3.04 °C, 33.10 psu, 17.10DIN, 1.78P, 50.35Si	− 0.84 °C, 31.99 psu, 5.48DIN, 1.37P, 19.83Si	− 0.48 °C, 32.15 psu, 2.30DIN, 1.04P, 16.08Si
75 m	1.97 °C, 33.17 psu, 16.68DIN, 1.61P, 60.60Si	0.98 °C, 32.46 psu, 7.65DIN, 1.74P, 56.20Si	− 0.93 °C, 32.12 psu, 3.83DIN, 1.86P, 48.69Si
75–100 m	1.97 °C, 33.17 psu, 18.85DIN, 1.83P, 59.36Si	1.64 °C, 32.66 psu, 7.93DIN, 1.85P, 69.38Si	− 0.95 °C, 32.04 psu, 3.60DIN, 1.60P, 44.06Si
> 100 m	2.27 °C, 33.46 psu, 24.78DIN, 2.11P, 72.75Si	2.11 °C, 32.88 psu, 7.62DIN, 2.42P, 70.18Si	ND
Average in water column	3.88 °C, 33.12 psu, 17.13DIN, 1.67P, 50.91Si	2.43 °C, 31.82 psu, 4.25DIN, 1.17P, 27.20Si	3.30 °C, 31.69 psu, 1.32DIN, 0.78P, 8.78Si

Table 2
The spatial variability of Chl *a* (mg/m^3) vertical distribution for each set of stations in the Bering Sea in July 2010.

Spatial	Basin	Slope	Shelf	Survey region
Stations	B01, B04, B06, B07, B11	B14, BB02	BB04, NB01, NB03, NB04, NB06, NB08, NB-A, BS02, BS05, BS08, BS11	18 stations in total
Depth (m)	2634–5860	93–137	24–59	24–5860
Surface	0.45, n = 5	0.18, n = 2	1.58, n = 11	1.11, n = 18
10 m	ND	0.30, n = 2	2.53, n = 11	2.19, n = 13
10–20 m	0.73, n = 5	0.37, n = 1	3.01, n = 11	2.18, n = 17
20–30 m	0.87, n = 5	1.65, n = 2	3.53, n = 10	2.53, n = 17
30–50 m	0.43, n = 5	0.43, n = 2	5.41, n = 7	2.93, n = 17
75 m	0.30, n = 5	0.16, n = 2	0.85, n = 2	0.39, n = 9
100 m	0.12, n = 5	0.11, n = 2	0.30, n = 2	0.16, n = 9
150 m	0.05, n = 2	0.09, n = 1	ND	0.06, n = 3
200 m	0.06, n = 4	ND	ND	0.06, n = 3
Average in water column	0.43, n = 35	0.55, n = 14	2.91, n = 54	1.82, n = 103

column varied greatly, ranging from 0.05 to 16.14 mg/m^3 with an average value of 1.82 mg/m^3 in all depths. Chl *a* concentrations differed significantly between regions, being highest in the Bering Shelf and lowest in the Bering Basin consistent with those of the nutrients (Fig. 2, Table 2). In particular, the water column Chl *a* concentration was only 0.43 mg/m^3 in stations across the Aleutian Islands and Bering Basin, while the maximum was found in the Bering Shelf, amounting to 2.91 mg/m^3. This was about 6.8 times higher than in the Bering Basin. On the Bering Slope, the water column Chl *a* was 0.55 mg/m^3, slightly higher than those in the Basin. On a regional scale, the water column Chl *a* in the Basin were not significantly different with those on the Slope, while those in the Shelf were significantly higher. Further, Chl *a* also decreased with depth but was still higher in the Shelf than the Slope and the open ocean. For example, Chl *a* in the upper 50 to 100 m depth in the Shelf was 3.3 times higher (1.84 mg/m^3) than at the Slope, while it was 6.3 fold higher in the upper 50 m depth with 3.48 mg/m^3.

A subsurface chlorophyll maxima (SCM) was found in most stations throughout the Bering Sea (Table 2) in between 20 m and 30 m depth. However, the SCM in the Slope appeared deeper than in the Basin where it mostly occurred at 30 m and deepest in the Shelf at 40 m to 50 m depth. In the first CHINARE cruise in the summer of 1999, Wang and Zhao (2011) showed that the thermocline and halocline in Bering Shelf were both stable and generally occurring at 15 m and 25 m. Kang et al. (2014) also suggested that the density differences in the upper waters in Bering Shelf were driven by thermal warming caused by solar radiation and freshening due to the melting of ice or land inputs. On the other hand, the stratification associated with the salinity differences of the different water masses influenced the distribution of Chl *a*. Specifically, it inhibited the transport of nutrients from the nutrient-rich deeper waters, resulting in nutrient drawdown and limitation in the surface, which in turn led to the establishment of the SCM in the nitracline at the top (below 50 m) of the Pacific Halocline (Tables 1 and 2). Usually, in the Bering Sea, underneath the surface or Polar Mix Layer (PML) is Pacific Summer Water (PSW) found between 60 and 100 m underlain by the Pacific Winter Water (PWW) from 100 to 200 m (Shimada et al., 2001).

3.3. Phytoplankton species composition

Phytoplankton communities were classified into 149 species belonging to 57 genera, and some unidentified species. Phytoplankton or photosynthetic species comprised 101 diatoms belonging to 38 genera, 44 dinoflagellates within 15 genera, 2 species of Chrysophyta, and 1 species for each Chlorophyta and Euglenophyta. Overall, the phytoplankton community was dominated by diatoms comprising 67.78%, with the rest composed of 29.53% dinoflagellates, 1.34% Chrysophyta, and 0.67% each Euglenophyta and Chlorophyta. Chlorophyta and Euglenophyta were only found in stations NB06 and NB08 near the coast of the Alaskan shelf, and might be more associated with freshwater input (Coachman, 1986). The most dominant dinoflagellates included *Amphidinium*, *Gymnodinium* and *Gyrodinium fusiforme*, while diatoms were dominated by *Navicula* spp., *Fragilariopsis* spp., *Neodenticula seminae*, *Leptocylindrus danicus*, *Pseudonitzschia delicatissima*, *Thalassiosira nordenskiöldii*, *Nitzschia closterium*, *Chaetoceros socialis*, *C. atlanticus* and *C. debilis*.

3.4. Abundance of phytoplankton

Patterns of abundance and horizontal distributions of phytoplankton followed that of the biomass (Fig. 3), and varied greatly from 1.17 × 10^3 cells/L to 333.30 × 10^3 cells/L (mean:127.27 × 10^3 cells/L). Mean cell abundance in the upper water column was also highest in the Shelf (147.06 × 10^3 cells/L), followed by the Slope (52.10 × 10^3 cells/L) and lowest in the Basin (10.22 × 10^3 cells/L). Boreal-temperate species such as *Chaetoceros debilis*, *C. socialis*, and the cosmopolitan species *Leptocylindrus danicus* were also found in high abundances in the Bering Shelf, together with cold-water species (*Thalassiosira nordenskiöldii*, *Fragilariopsis cylindrus* and *F. oceanica*) which thrive in the Alaska coast (Station NB08) and near the Bering Strait (Stations BS02, BS05 and BS08).

Phytoplankton abundances were also found to be highest in the SCM (Table 3, Fig. 4) with marked spatial variation (Table 3). Abundance peaks were deeper in the Shelf than the Basin. In the Bering Basin, the highest value was found between 10 m and 20 m depth (Table 3). This was different from the vertical distribution of biomass in the Shelf (Table 2) where the abundance peaks were shallower than maximum chl *a* concentrations. In the Slope, the abundance peak was close to 30 m and was similar to chl *a* (Table 2). In the Shelf, the decoupling of

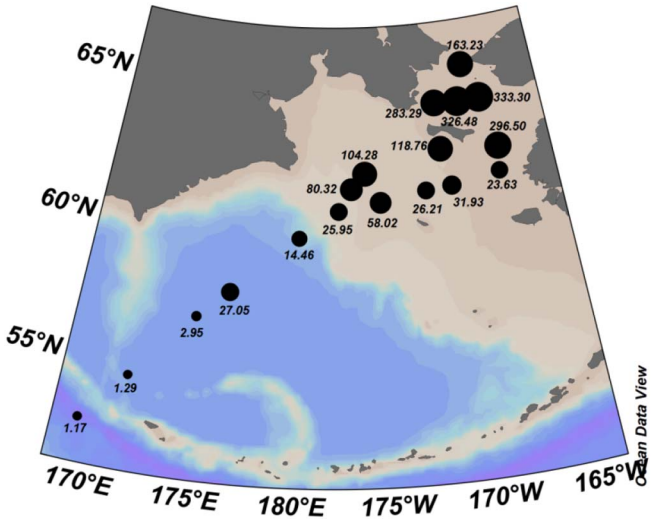

Fig. 3. Spatial distribution of average abundance (× 10^3 cells/L) in water column for each set of stations in the Bering Sea in July 2010.

Table 3
The spatial variability of abundance ($\times 10^3$ cells/L) and vertical distribution for each set of stations in the Bering Sea in July 2010.

Spatial	Basin	Slope	Shelf	Survey region
Stations	B01, B04, B06, B07, B11	B14, BB02	BB04, NB01, NB03, NB04, NB06, NB08, NB-A, BS02, BS05, BS08, BS11	18 stations in total
Depth (m)	2634–5860	93–137	24–59	24–5860
Surface	12.16, n = 5	37.34, n = 2	68.66, n = 11	58.72, n = 18
10	ND	55.98, n = 2	128.96, n = 11	117.73, n = 13
10–20 m	36.05, n = 3	124.55, n = 1	220.93, n = 11	177.53, n = 15
20–30 m	23.69, n = 4	185.00, n = 1	180.33, n = 7	128.50, n = 12
30–50 m	5.98, n = 6	66.74, n = 4	216.77, n = 7	117.49, n = 21
50–100 m	1.87, n = 8	4.38, n = 4	12.17, n = 4	5.07, n = 16
> 100 m	0.44, n = 5	0.73, n = 1	ND	0.48, n = 6
Average in water column	10.22, n = 31	52.10, n = 15	147.06, n = 51	127.27, n = 97

peaks of the abundance and chl *a* were more apparent. Abundance maxima was found in the upper 20 m of the water column when the bottom depth was shallower than 30 m, while it was consistently found at 30–50 m depth when the bottom depth was deeper than 50 m.

In the Bering Basin, the peak abundance was observed along the thermocline based on comparisons made with salinity, temperature and nutrient (DIN + P + Si) profiles (Table 1, Fig. 4), while it was mostly associated in the haloclines in the Slope and Shelf (Table 1, Fig. 4).

3.5. Community structure and geographic range

Results of MDS showed that phytoplankton taxa could be grouped into two communities, namely deep-sea and neritic assemblages with an approximately 36% similarity between each other (Fig. 5). The deep-sea assemblage (assemblage I, Fig. 5) was found in the Bering Basin and mainly composed of boreal-temperate marine species, including *Neodenticula seminae*, *Chaetoceros atlanticus*, and cosmopolitan species, including *Pseudonitzschia delicatissima*, *Thalassionema nitzschioides*, among

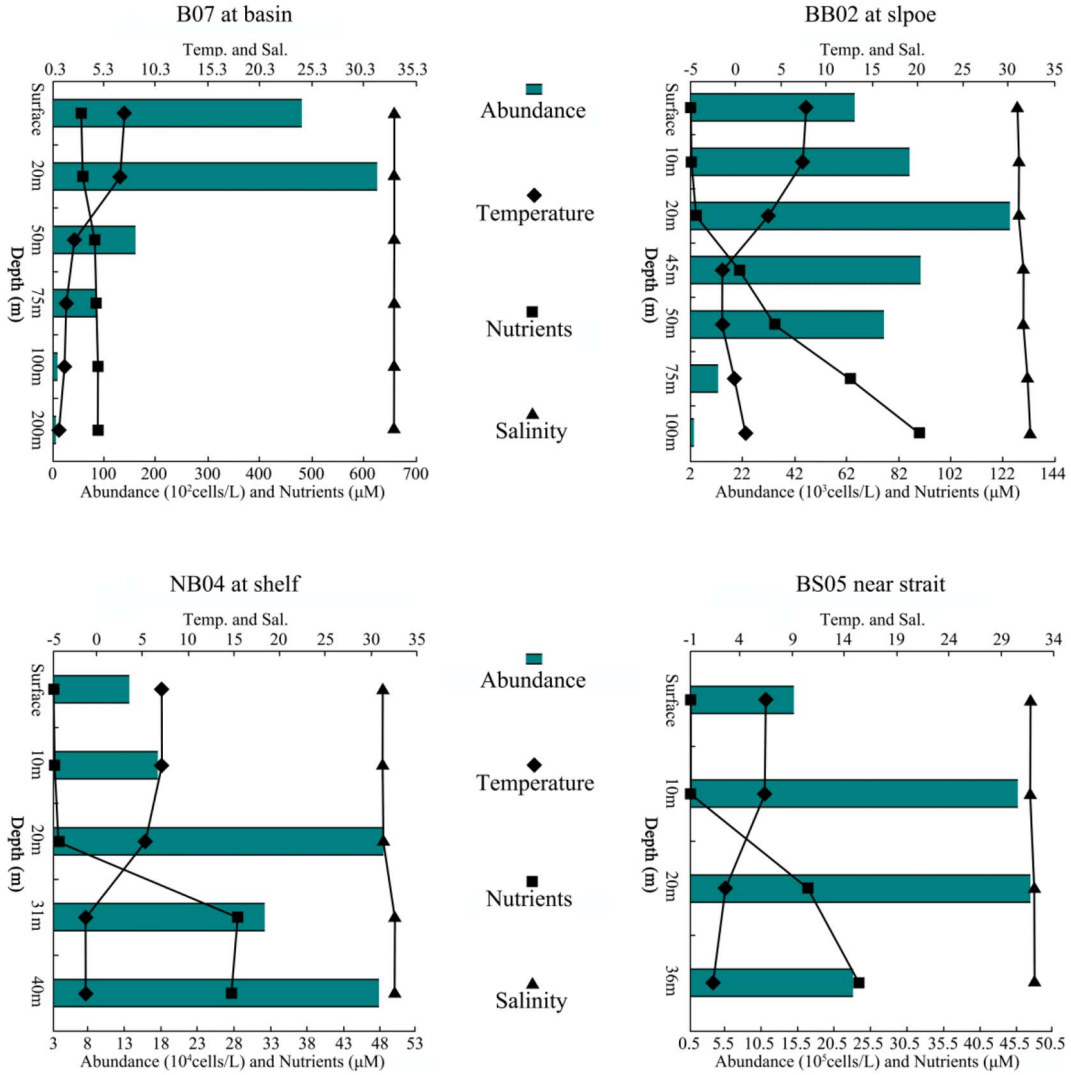
B07 at basin
Temp. and Sal.
0.3 5.3 10.3 15.3 20.3 25.3 30.3 35.3
Surface 20m 50m 75m 100m 200m
Depth (m)
0 100 200 300 400 500 600 700
Abundance (10^2cells/L) and Nutrients (μM)
Abundance
Temperature
Nutrients
Salinity
BB02 at slpoe
Temp. and Sal.
-5 0 5 10 15 20 25 30 35
Surface 10m 20m 45m 50m 75m 100m
Depth (m)
2 22 42 62 82 102 122 144
Abundance (10^3cells/L) and Nutrients (μM)
NB04 at shelf
Temp. and Sal.
-5 0 5 10 15 20 25 30 35
Surface 10m 20m 31m 40m
Depth (m)
3 8 13 18 23 28 33 38 43 48 53
Abundance (10^4cells/L) and Nutrients (μM)
BS05 near strait
Temp. and Sal.
-1 4 9 14 19 24 29 34
Surface 10m 20m 36m
Depth (m)
0.5 5.5 10.5 15.5 20.5 25.5 30.5 35.5 40.5 45.5 50.5
Abundance (10^5cells/L) and Nutrients (μM)

Fig. 4. Vertical distribution of phytoplankton abundance and environmental correlates at exemplary stations in the Bering Sea in July 2010. Stations B07 located in Bering Basin, BB02 in Bering Slope, NB04 and BS05 in Bering Shelf. The top axis indicated water temperature (°C) and salinity. The bottom axis indicated nutrients (DIN + P + Si) (μM) and phytoplankton abundance of 10^2 cells/L at station B07, 10^3 cells/L at station BB02, 10^4 cells/L at station NB04, and 10^5 cells/L at station BS05, respectively.

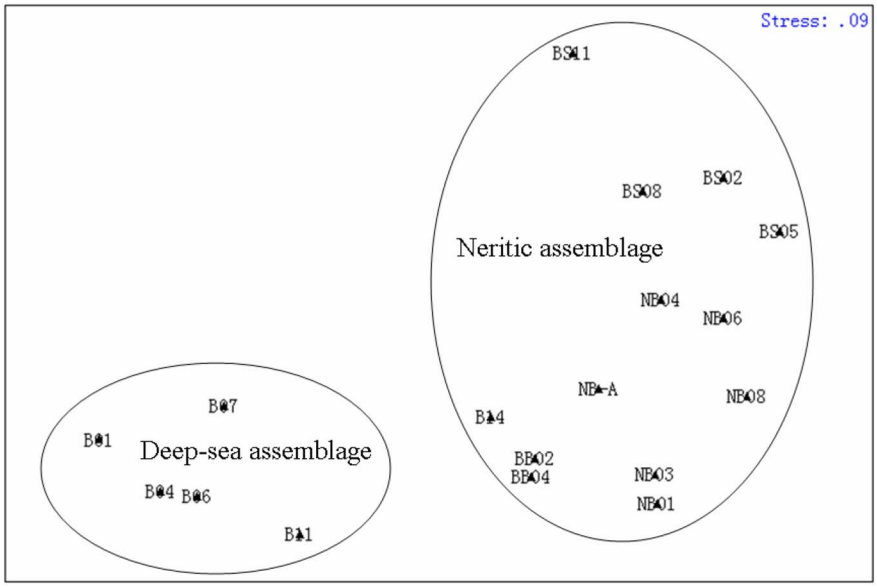

Fig. 5. Multi-Dimensional Scaling (MDS) ordination of phytoplankton assemblages in the surface layer for each set of stations of the Bering Sea in July 2010.

others. The average phytoplankton abundance and biomass of the deep-sea assemblage were only 10% and 17% respectively, than that of the neritic assemblage. However, because there was no prominent dominant species and the abundance was evenly distributed among species ($J' = 0.69$), the species diversity index (H') was higher than species richness (d).

The neritic assemblage (assemblage II, Fig. 5) on the other hand was associated with the shallower waters in Bering Slope and Shelf, and mostly composed of cold-water species such as *Thalassiosira nordenskiöldii*, *Fragilariopsis oceanica*, *Chaetoceros furcellatus*, *C. socialis* and cosmopolitan species *Leptocylindrus danicus*, *C. curvisetus*, *Nitzschia closterium*. Phytoplankton total abundance and biomass were generally $> 1.00 \times 10^5$ cells/L and 1.00 mg/m^3, respectively. However, because of the uneven distribution of abundance among species ($J' = 0.51$) and the existence of highly dominant taxa, the species diversity index (H') was significantly lower than the deep-sea assemblage while species richness (d) was higher (Table 4).

3.6. Dominant species and distribution

The distribution of the dominant species varied significantly in stations (Fig. 6). For example, *Neodenticula seminae* was generally low in the surface layers in all stations (Table 4). It was highest in the Bering Basin and Slope but was significantly low in the Shelf (Fig. 6a), and its presence in the Bering Sea was consistent with the intrusion of the North Pacific Ocean waters declining towards the Bering Shelf (e.g. NPO; Simonsen and Kanaya, 1961; Shimada et al., 2006; Onodera et al., 2005). The same was true for the cosmopolitan species *Pseudonitzschia delicatissima* (Fig. 6b), the presence of which in the Bering Sea has been suggested to indicate the strong hydrographic events in the system (Kawarada, 1957).

Leptocylindrus danicus is an important cosmopolitan species found in the Arctic seas (Werner, 1977; Heimdal, 1989; Melnikov, 1997) and was found throughout the Bering Shelf and Slope with the greatest abundances in the nearby Bering Strait, but was rarely found in Bering Basin during this study (Fig. 6c). The cold-water species *Thalassiosira nordenskiöldii* was also widely found in Bering Shelf, with the highest counts in station BS11 located at the Bering Strait but was absent in the Bering Basin (Fig. 6d). It was mainly identified with cold waters (Hasle and Syvertsen, 1997) and was the main dominant species in Bering and Chukchi Seas during spring (Irina et al., 2009; Wang, 2009).

Table 4
Comparison of phytoplankton assemblages and environmental correlates for each set of stations in the Bering Sea in July 2010.

Phytoplankton assemblages	Deep-sea assemblage	Neritic assemblage
Spatial Stations	Bering Basin B01, B04, B06, B07, B11	Bering Slope and Shelf B14, BB02 in Slope, BB04, NB01, NB03, NB04, NB06, NB08, NB-A, BS02, BS05, BS08, BS11 in Shelf
Salinity	Mean: 33.12 Range: 32.61–33.91	Mean: 31.73 Range: 30.28–32.88
Temperature (°C)	Mean: 3.88 Range: 0.87–8.26	Mean: 3.01 Range: − 1.48-8.31
DIN (μM)	Mean: 17.13 Range: ND-31.23	Mean: 6.20 Range: ND-29.88
PO_4-P (μM)	Mean: 1.67 Range: 0.16–2.99	Mean: 0.87 Range: 0.09–2.42
SiO_3-Si (μM)	Mean: 50.91 Range: 3.08–98.01	Mean: 12.82 Range: ND-70.18
Biomass (mg/m^3)	Mean: 0.43 Range: 0.05–1.79	Mean: 2.41 Range: 0.09–16.14
Abundance (10^3 cells/L)	Mean: 10.22 Range: 0.12–62.5	Mean: 127.27 Range: 0.73–568.63
Specie richness (d) in surface layer	Mean: 1.66 Range: 1.49–1.95	Mean: 2.55 Range: 1.89–3.21
Pielou's evenness (J') in surface layer	Mean: 0.69 Range: 0.43–0.89	Mean: 0.51 Range: 0.33–0.72
Diversity (H') in surface layer	Mean: 2.60 Range: 1.93–3.18	Mean: 2.41 Range: 1.63–3.14
Dominant species (Y) in surface layer	*Neodenticula seminae* (0.43), *Pseudonitzschia delicatissima* (0.31), *Chaetoceros atlanticus* (0.05), *Thalassionema nitzschioides* (0.02)	*Leptocylindrus danicus* (0.46), *Thalassiosira nordenskiöldii* (0.10), *Nitzschia closterium* (0.05), *Fragilariopsis oceanica* (0.02), *Chaetoceros socialis* (0.02), *Pseudonitzschia delicatissima* (0.02), *Chaetoceros debilis* (0.02)

3.7. Correlation between phytoplankton and environmental conditions

Pearson's correlation analysis (Table 5) showed a negative correlation between biomass and nutrients (NO_3-N, PO_4-P and SiO_3-Si) in the water column of the Bering Basin, while phytoplankton abundance was only negatively correlated with silicate concentration. In contrast, in the Bering Slope, no significant correlations were found between

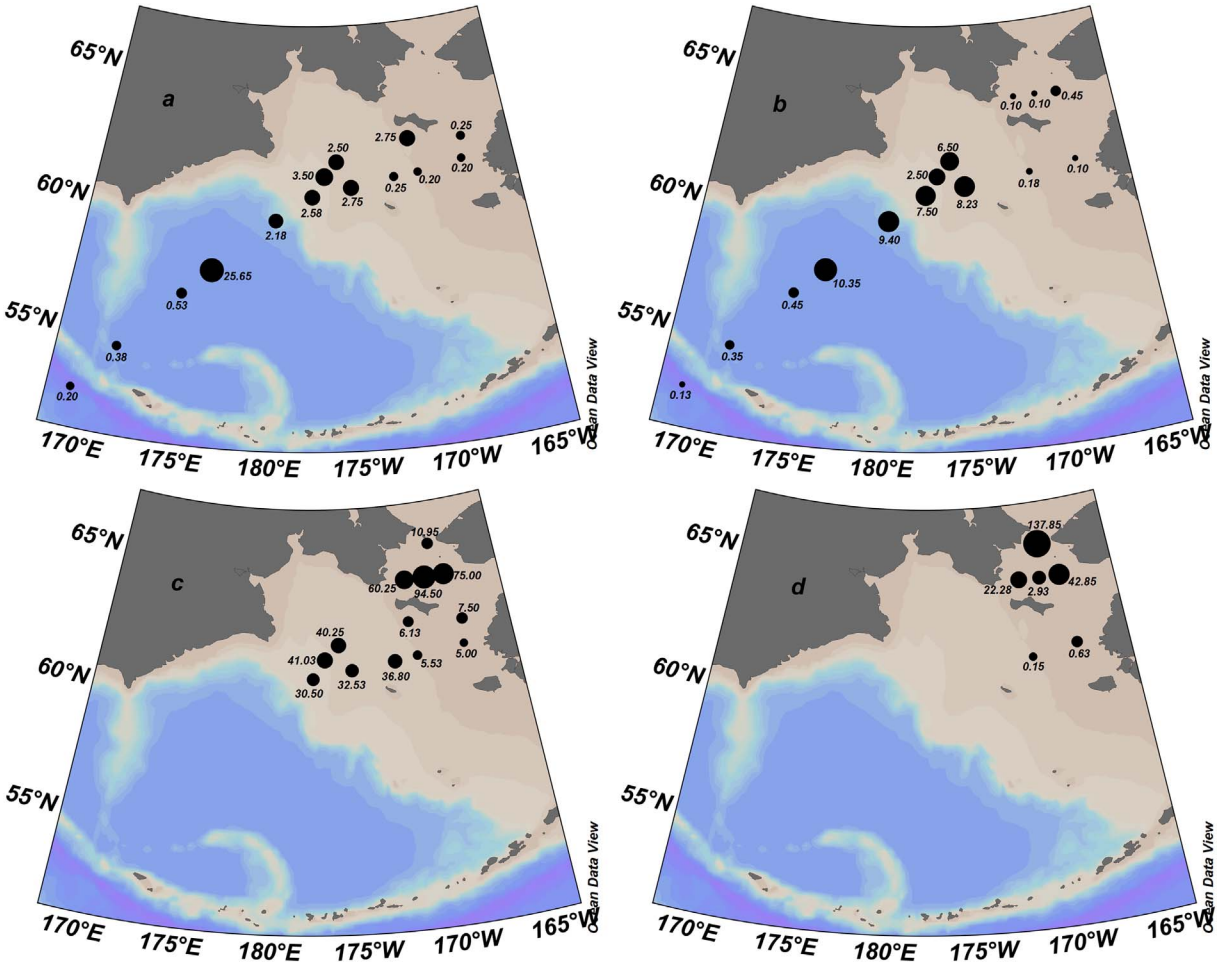

Fig. 6. Spatial distribution of abundance ($\times 10^3$ cells/L) of exemplary dominant species in the surface layer of the Bering Sea in July 2010, e.g. showing a: *Neodenticula seminae*, b: *Pseudonitzschia delicatissima*, c: *Leptocylindrus danicus*, d: *Thalassiosira nordenskiöldii*.

Table 5
Pearson correlation analysis between phytoplankton biomass, abundance and environmental factors in water columns of the Bering Sea in July 2010.

Region	Parameters		Biomass	Temperature	Salinity	NO_3-N	NO_2-N	NH_4-N	PO_4-P	SiO_3-Si
Bering basin	Biomass	Coefficient	–	0.310	−0.556**	−0.403*	–	–	−0.408*	−0.591**
		Significance	–	0.090	0.001	0.024	–	–	0.023	0.000
		Samples	–	31	31	31	–	–	31	31
	Abundance	Coefficient	0.514**	0.377*	−0.249	−0.258	–	–	−0.234	−0.371*
		Significance	0.003	0.036	0.177	0.162	–	–	0.188	0.040
		Samples	31	31	31	31	–	–	31	31
Bering slope	Biomass	Coefficient	–	−0.514	−0.062	−0.082	−0.472	0.376	−0.009	−0.321
		Significance	–	0.050	0.827	0.771	0.075	0.167	0.975	0.244
		Samples	–	15	15	15	15	15	15	15
	Abundance	Coefficient	0.485	−0.135	−0.588*	−0.681**	−0.056	−0.090	−0.424	−0.663**
		Significance	0.067	0.632	0.021	0.005	0.842	0.751	0.115	0.007
		Samples	15	15	15	15	15	15	15	15
Bering shelf	Biomass	Coefficient	–	−0.279*	0.541**	0.347**	0.486**	0.010	0.197	0.110
		Significance	–	0.036	0.000	0.010	0.000	0.948	0.142	0.414
		Samples	–	57	57	55	48	48	57	57
	Abundance	Coefficient	0.400**	−0.088	0.278*	0.1821	0.154	−0.040	−0.013	−0.166
		Significance	0.002	0.516	0.036	0.183	0.297	0.789	0.926	0.216
		Samples	57	57	57	55	48	48	57	57

** Correlation is significant at the 0.01 (2-tailed).
* Correlation is significant at the 0.05 (2-tailed).

phytoplankton biomass and nutrients, while phytoplankton abundance was negatively correlated with SiO_3-Si and NO_3-N. In the shelf, biomass was significantly positively correlated with both NO_3-N, and NO_2-N, and phytoplankton abundance was only positively correlated with salinity.

A CCA biplot of dominant species and environmental parameters is presented in Fig. 7. The upper right section represented the waters with high nutrient concentrations and high salinity in the Bering Basin, where abundances of *Chaetoceros atlanticus*, *Pseudonitzschia delicatissima*, *Neodenticula seminae* and *Thalassionema nitzschioides* all had

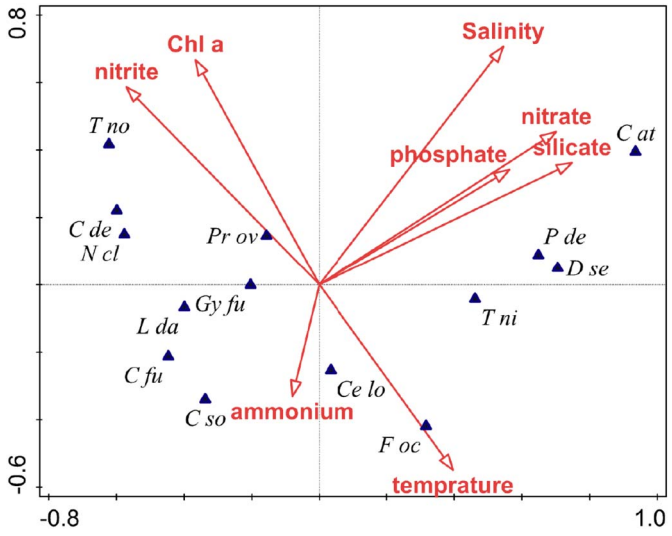

Fig. 7. Canonical correspondence analysis of the dominant phytoplankton species and environmental parameters in the surface layer of the Bering Sea in July of 2010. Arrows with different lengths denote relative correlations of different independent variables with the biological factors: temperature, salinity, nitrate, nitrite, ammonium, phosphorous, silicate, and chl *a* concentration. The abbreviated names for phytoplankton are: *C at*, *Chaetoceros atlanticus*; *C de*, *Chaetoceros debilis*; *C so*, *Chaetoceros socialis*; *C fu*, *Chaetoceros furcellatus*; *D se*, *Neodenticula seminae*; *L da*, *Leptocylindrus danicus*; *F oc*, *Fragilariopsis oceanica*; *N cl*, *Nitzschia closterium*; *P de*, *Pseudonitzschia delicatissima*; *T ni*, *Thalassionema nitzschioides*; *T no*, *Thalassiosira nordenskiöldii*; *Ce lo*, *Ceratium longipes*; *Gy fu*, *Gyrodinium fusiforme*; *Pr ov*, *Protoperidinium ovum*.

positive correlation with nutrient concentrations. Meanwhile, the left quadrat in the biplot indicated the habitats in the Bering Slope and Shelf characterized by low nutrient concentrations and high temperature. In these waters, dinoflagellates such as *Ceratium longipes*, *Gyrodinium fusiforme*, and *Protoperidinium ovum* showed strong association with high concentrations of nitrite and ammonium. In contrast, diatoms like *Chaetoceros debilis*, *Nitzschia closterium*, *Leptocylindrus danicus*, *Chaetoceros furcellatus*, *and Chaetoceros socialis* were only weakly correlated with those nutrients. Lastly, some species were associated with opposite temperature conditions, for example, *Fragilariopsis oceanica* with high temperature and *Thalassiosira nordenskiöldii* with the cold.

4. Discussion

4.1. Phytoplankton biomass variability and its environmental controls

Despite the high availability of nutrients in the Bering Basin, phytoplankton biomass remained low. Such conditions are usually referred to as high nutrient and low Chl *a* (HNLC) conditions (Banse and English, 1999). Previous studies indicated that the surface phosphate and silicate concentrations in Bering Basin were generally high, but were not the limiting factors for phytoplankton photosynthesis (Mordasova et al., 1995; Niebauer et al., 1995). HNLCs are thought to be limited by the presence of micronutrient Iron (Fe^{2+}) that is important for photosynthesis, which then limits the growth of phytoplankton. Bering Basin was highly similar to the Northeast Pacific waters, partly due to the Alaskan Coastal Current that goes through the channel of the Aleutian Islands leading to the Bering Basin (Fig. 1; Koide et al., 2001). This suggests then that the transport of water masses could also influence the distribution of phytoplankton in the Bering Basin.

Arsen'ev (1967) used 5800 hydrological profiles collected from 1874 to 1959 to demonstrate that there was a fast and wide current that passes from the southeast to northwest of Bering Slope. These currents have been suggested to result in low nutrient, low pCO_2, high pH, and high Chl *a* surface waters (Chen et al., 2003). Consequently, Bering Sea Green Belt (BSGB) waters were observed to have higher biomass than the Bering Basin. Gao et al. (2011) suggested that waters in the Bering Slope were silicate-limited because of high absorption by diatoms. However, no significant correlations were found between phytoplankton biomass and nutrients (Table 5). In contrast to the observations of Gao et al. (2011), we did not assume that phytoplankton biomass was limited by SiO_3-Si concentration in the Bering Slope in the summer of 2010 (Table 5). Kang et al. (2014) also suggested that SiO_3-Si concentration was an occasional factor, which influenced phytoplankton phytosynthesis in the Bering Slope, while hydrographic variations were the major factor influencing phytoplankton biomass variations.

On the Bering Shelf, biomass was significantly positively correlated with both NO_3-N, and NO_2-N (Table 5), despite previous reports that Bering Shelf was significantly nitrogen-limited (Niebauer et al., 1995; Gao et al., 2011). Nutrient addition experiments in the upper and deeper waters showed that NO_3-N was more absorbed than PO_4-P, suggesting an N-driven limitation in the Shelf (Tyrrell, 1999; Zhang et al., 2000) with conclusions of much more NO_3-N than PO_3-P could be absorbed by phytoplankton. Moreover, biomass also increased with salinity over the Bering Shelf (Table 5). Yang and Lin (2006) suggested that Arctic and boreal-temperate phytoplankton, which were widely distributed in the Bering Shelf, are more adapted and could thrive well in low temperature and high salinity conditions.

4.2. Phytoplankton abundance distribution and environmental drivers

In the Bering Sea, interactions between the Siberian High and the Aleutian Low determine regional changes in circulation and thermal profiles (Luchin et al., 2002). While ice melting changes the salinity and temperature at the ice edge which could strengthen stratification, at times, wind-driven upwelling may also take place (Alexander and Niebauer, 1981; Koide et al., 2001). Upwelling brings nutrients to surface waters, potentially enhancing production depending on light availability. In this study, phytoplankton abundance increased dramatically at Stations B07 and B11, mostly towards the central Bering Basin (Fig. 3) where dense populations of *Neodenticula seminae*, *Pseudonitzschia delicatissima* and *Chaetoceros atlanticus* were observed. Additionally, the sea ice retreat from spring to summer resulted to spring blooms, accounting for the highest abundance observed in the Bering Shelf compared to that of in the Bering Slope and Basin (Fig. 3).

In addition, the spatial distribution of phytoplankton abundance in the summer of July 2010 was opposite to that during a spring expedition in the Bering Sea (e.g. Wang, 2009; Sei-ichi et al., 2002). Analysis of 2008 spring cruise from the United States showed that the lowest phytoplankton abundance was near the St. Lawrence Island to the north near the Bering Strait (Wang, 2009), whereas the highest abundance observed was in the open waters of the Bering Basin. This difference in observations was strongly related to seasonal variability since the two studies were conducted at different periods of the year.

Phytoplankton abundance in the Bering Sea has been previously reported to vary both geographically and seasonally, and phytoplankton blooms were dependent on the location and time of the retreat of sea ice (McRoy et al., 1972; Veth et al., 1992; Hunt et al., 2002). In spring, the high-temperature and high-salinity waters from the northern Pacific Ocean causes sea ice to retreat from the southwest towards the northeast, resulting in earlier temperature rises in the Bering Basin (Lovvorn et al., 2009; Grebmeier et al., 2006). Consequently, the warmer water and increased transmissivity favors the “seeding” effect of ice algae causing blooms to occur around the edge of melting glaciers (Schandelmeier and Alexander, 1981; Niebauer and Alexander, 1985). During July of 2010, phytoplankton abundance could not generate high density blooms despite the large amount of nutrients in the Bering Basin (Tables 3 and 4, Fig. 3). In contrast, the Bering Shelf waters became warmer and fresher due to ice loss and land inputs, and increased solar radiation, with higher nutrients due to mixing. These conditions were optimal for phytoplankton growth, leading to a bloom period of

explosive reproduction, particularly in the Bering Strait (Figs. 2 and 3) (e.g. Sei-ichi et al., 2002; Liu et al., 2011; Kang et al., 2014).

4.3. Phytoplankton species distribution properties and its environmental controls

Phytoplankton species showed a strong biogeography in the Bering Sea (Motoda and Minoda, 1974; Heimdal, 1989). The arctic species (e.g. *Thalassiosira nordenskiöldii*, *Fragillaria crotonensis*, *Fragilariopsis cylindrus*, *Chaetoceros furcellatus*) belonging to the neritic Assemblage (Fig. 5) were found abundant in the Slope and Shelf, mainly in the surface layer of the western Bering Sea along the Siberian coast (Motoda and Minoda, 1974; Werner, 1977). In particular, *Thalassiosira nordenskiöldii* was abundant but limited to the Bering Strait (station BS11) while *Chaetoceros furcellatus* was mainly present in the Shelf and Slope but absent in the Basin. *Fragilariopsis oceanica*, first thought to be limited to the high-latitude Arctic waters, was found to be also common in the Bering Sea, Okhotsk and Chukchi Seas (Sancetta, 1982), but more prominently in sea ice communities (Hasle and Syvertsen, 1997; Irina et al., 2009). Due to seasonal sea ice formation in the Shelf, the ice-associated species *Nitzschia frigid* was also found among the phytoplankton, although in lower numbers in the water during summer. The commonly reported Arctic sea ice diatom *Melosira arctica* (Boetius et al., 2013) was not observed in this study area.

Boreal-temperate species made up the majority of phytoplankton taxa in the Bering Sea. These species were more abundant in the Bering Basin during the survey. Their distribution was directly related to the intrusion of warmer and highly saline waters from the northern Pacific Ocean to the Bering Sea (Yang et al., 2002; Shimada et al., 2003; Katsuki and Takahashi, 2005).

Different species dominated in different depths, suggesting environmental filtering or adaptations (Table 6). For example, the surface layer was mainly composed of centric diatom. On the other hand, the SCM was dominated by pennate diatoms. The deeper waters were mainly populated by dinoflagellates.

4.4. Influences of previous spring sea ice retreat on summer phytoplankton in Bering Sea

Seasonal sea ice is one of the most defining features of the subarctic Bering Shelf, influencing both the physical and biological structure of the water column not only during periods of ice cover but throughout the year (Hunt et al., 2008; Stabeno et al., 2010, 2012). Previous studies have shown that ice algae may continue growing in the water column after ice retreat, seeding the spring phytoplankton blooms and further extending their importance in the ecosystem (e.g., Michel et al., 1993; Haecky et al., 1998). For the Bering Sea, this hypothesis has been supported by ecosystem modeling studies (Jin et al., 2007) and observations of marginal ice zone blooms (Schandelmeier and Alexander, 1981).

Table 6
Phytoplankton species distribution properties illustrated by major and common species in various depth layers for each set of stations of the Bering Sea in July 2010, suggesting environmental filtering or adaptations of controls.

Water layers	Major and common species in the survey region
Surface	*Neodenticula seminae*, *Chaetoceros socialis*, *Nitzschia closterium*, *Chaetoceros atlanticus*, *Leptocylindrus danicus*, *Pseudonitzschia delicatissima*, *Thalassiosira nordenskiöldii*
10 m	*Neodenticula seminae*, *Thalassionema nitzschioides*, *Thalassiosira nordenskiöldii*, *Chaetoceros curvisetus*, *Pseudonitzschia delicatissima* *Chaetoceros debilis*
10–30 m	*Chaetoceros furcellatus*, *Chaetoceros socialis*, *Thalassiosira nordenskiöldii*, *Fragilariopsis oceanica*, *Fragilariopsis cylindrus*
30–50 m	*Achnanthes taeniata*, *Fragilariopsis oceanica*, *Fragilariopsis cylindrus*, *Nitzschia frigida*
> 50 m	*Gyrodinium fusiforme*, *Protoperidinium* spp., *Navicula* spp.

Mordasova et al. (1995) suggested that phytoplankton blooms usually occur in spring because of nutrient repletion and seeding of the ice algae released from sea ice. They also further argued that another bloom is not even possible after spring due to nutrient limitation. However, in this study, a diatom bloom was observed at station BS11 of the Bering Strait with 6.47 mg/m^3 and 1.92 × 10^5 cells/L of biomass and cell counts, respectively in the surface layer and 16.14 mg/m^3 at the 10 m layer. The surface waters in BS11 had 4.59 °C, salinity of 32.32, DIN (0.46 μmol/L), and silicate (1.56 μmol/L), which were higher than the average of those in the Slope, except for phosphate (0.34 μmol/L), which was highly similar to the Basin.

Historically in the summer of 2008, a high Chl *a* (22.41 mg/m^3 at the surface layer, 30 mg/m^3 at the 10 m layer) was also found near the Bering Strait (Liu et al., 2011). This indicates that phytoplankton blooms also appear frequently in summer in the Bering Sea after ice retreat.

The sea ice retreat during spring also influenced species composition of pelagic diatoms in the Bering Sea. Zhou et al. (2015) reported pennate diatoms of the genera *Grammonema* and *Fragillariopsis* to dominate in May in Bering Shelf. Spring phytoplankton communities also showed increasing dominance of ice-associated species with proximity to the ice edge (Schandelmeier and Alexander, 1981). There was also an apparent shift from pennate to centric diatom dominance from spring to early summer (Taniguchi et al., 1976), when dense populations of *Thalassiosira nordenskiöeldii*, *T. hyalina* and *Fragilariopsis* spp. were observed. In this study, ice-associated species were replaced by pelagic centric diatoms such as *T. nordenskiöeldii*, *C. furcellatus* and *C. socialis*, which were abundant in Bering Shelf and Slope, although some pennate species (e.g. *Fragilariopsis cylindrus*, *F. oceanica*, and *Navicula* spp.) were still found in high abundances in the water column even in the deeper layer (Table 6). After sea ice retreat, blooms of *T. nordenskiöeldii* spread near the Bering Strait (Fig. 6d) suggesting that ice-associated species could serve as seedbanks ensuring the succession of pelagic phytoplankton population in the subarctic ecosystem.

Data from the US National Snow and Ice Data Center (US NSIDC) showed that the Bering Sea is seasonally covered by sea ice. In the winter of 2010, however, only 75% of the shelf area was covered by sea ice, with the highest extent occurring at the end of March (Fig. 8) extending to the 200 m isobaths near Bristol Bay and Kamchatka offshore in the South. Consequently, during the summer of 2010 and 4th CHINARE, the Bering Sea was almost ice free (Fig. 8), and ice was hardly found to the south of 75.37°N at the end of August. It is predicted that some of the usually perennially covered shelf areas will be ice-free in the future, and could possibly favor the growth and reproduction of phytoplankton leading to increased primary productivity. In conclusion, the observed variation in both biomass and diversity of summer phytoplankton community in the Bering Sea was mostly influenced by events related to the spring sea ice retreat that year.

5. Conclusions

The subarctic Bering Sea is undergoing significant ecological shifts possibly linked to global climate change. Our current understanding of the CHINARE observed fluctuation in both biomass and summer phytoplankton communities are a support of environmental controls on phytoplankton spatial variability in the Bering Sea. A marked spatial zonation relative to taxonomic composition, abundance and biomass was found. There were two types of assemblages, one a deep-sea assemblage associated with Bering Basin and a neritic assemblage found in Bering Slope and Shelf. The vertical distribution of biomass and abundance demonstrated a distinctive subsurface maximum close to the thermocline and halocline. It was observed that a diatom bloom appeared near Bering Strait in summer associated with the spring sea ice retreat that year of 2010. Phytoplankton biomass was directly controlled by high availability of nitrate particularly in Bering Shelf, while

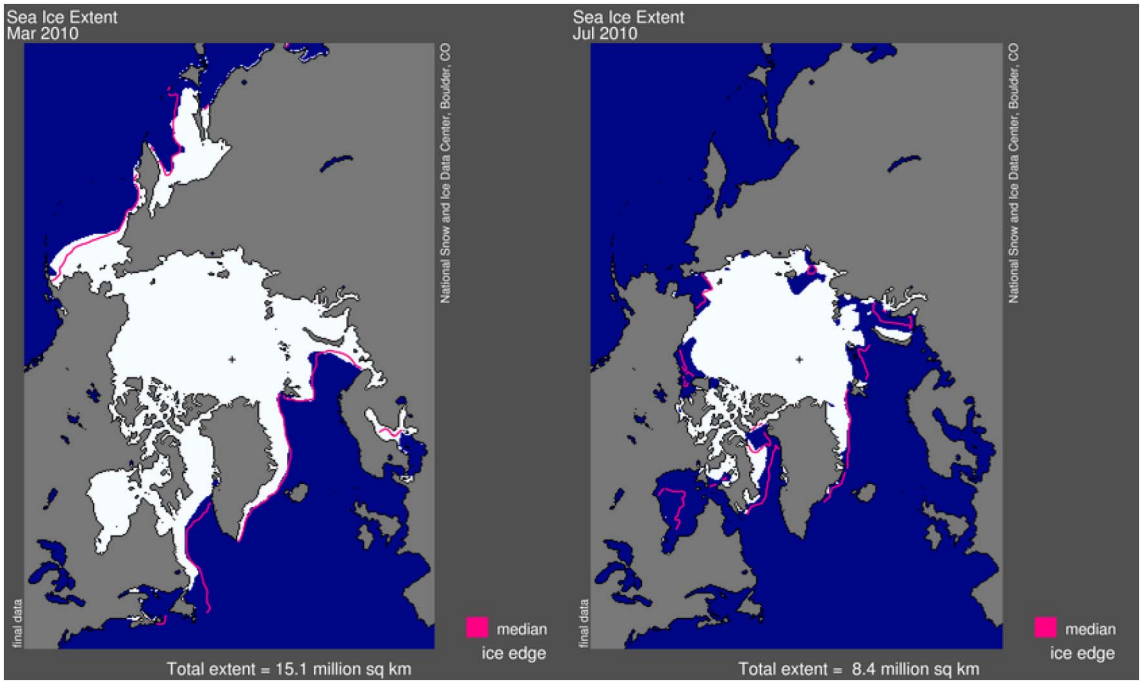

Fig. 8. Extent of the Arctic sea ice in March and July 2010. The small pink curve represents the median periglacial line in March and July of the Arctic Ocean in 2010 respectively, while the white indicates the coverage range of sea ice. These data are taken from the US National Snow and Ice Data Center, http://nsidc.org/. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

water mass transportation mainly influenced communities in Bering Basin and Slope.

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